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On the anomalous splitting of the rhizome and root of Delphinium scaposum

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(WITH PLATES 13 and 14)

Delphinium scaposum, first named by Greene,* is one of the xerophytic forms of the Ranunculaceae. The material used in this investigation was collected at the Desert Laboratory at Tucson, Arizona, under the kind direction of Dr. D. T. MacDougal of the Carnegie Institution. It was carefully killed at that time, and proved most satisfactory for anatomical study.

As to its distribution, Huth,† who names it *Delphinium decorum β scaposum* (Greene) Huth, reports that it was mentioned by Parry, 1874, as found in southern Utah, and by Pringle, 1883, in the Arizona hills near Tucson, the same territory from which this material was sent. Greene records its presence in the hill country between the Gila and San Francisco rivers, May 25, 1880, and says that Dr. Asa Gray informed him that Professor Newberry obtained what appeared to be the same, south of the Diamond River in Arizona.* In this same account, Greene gives the only adequate description of the plant, which I quote in part, as I have no acquaintance with the living form. "Leaves all radical, rather fleshy, pubescent, 3-parted, the divisions broadly cuneate, 3–5-cleft or toothed, the teeth ending in a callous point, racemose at summit, pedicels as long as the deep azure flowers; spur incurved, root a

*E. L. Greene. New Species of Plants from New Mexico. Bot. Gaz. **6**: 156–158. 1881.

†Ernst Huth. Die Delphinium-Arten der Vereinigten Staaten von Nord-Amerika. Abhand. und Vorträge Gesammtgeb. Naturw. **4**[3]: 9. 1892.

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cluster of thickened fleshy fibres. . . . An interesting species as combining the leafless stem of the scarlet flowered Californian *D. rudicaula* with the deep blue flowers of *D. azureum*."

The aerial part consists of leaves whose long petioles arise spirally from a restricted underground shoot, and blossoms borne on long stalks. These flourish in the brief rainy season and then die back, and the next year's leaves and flowers originate from a terminal bud, or from buds found one in the axil of each foliage leaf. The perennial part of the plant is subterranean, and is of the nature of a rhizome with roots attached. This is the part that was particularly studied here.

On examination of this portion of the plant body, of several different specimens, the most apparent characteristic common to all is the splitting up into separate members of the rhizome and root (FIG. 1). There is no regularity about the number or arrangement of the resulting columns, nor is their origin as separate individuals at an equal distance from the base of the annual shoot. In one case a specimen will appear like a miniature tree trunk covered with a dark brown barklike formation which easily crumbles off. This trunk continues down as one united column for an inch, and then abruptly divides into two unequal parts. If a cross section of the main trunk were examined immediately before this separation (FIG. 2) it would show a peripheral circle made up of single columns (in cross section), the central space and divisions between which are filled with this same loose brown necrotic tissue that surrounds the outside. Shallow grooves can be distinguished running longitudinally along the trunk, and continuing more deeply cleft in each of the two divisions, so that the first consists apparently of four, the second of seven united columns.

Following these two divisions down a short distance, we find them resolving themselves into their component members, or groups of two or three, and separating from each other. Each of these ultimate branches may continue as it is, or may later divide after it has attained a certain secondary growth in thickness. Occasionally a splitting apart occurs for a short distance and is followed by a complete union of these same members into one strand, which leads to the just conclusion that the phenomenon is one of splitting of mature organs rather than a peculiarity in

FIG. 1. Rhizome and root (natural size), showing where successive cross sections are taken.

FIG. 2. Cross section as indicated on FIG. 1, showing origin of separate columns. Necrotic central region.

regular growth development. Consequently, the whole appearance of the underground part of *Delphinium scaposum* is that of a highly complicated "cluster of fleshy roots" in part of their extent bound together like a cable, in part ramifying about irregularly through the soil and thus obtaining a wide spread. In another specimen, splittings occur almost immediately below the annual shoot. These split-off pillars need not necessarily be circular in cross section, for as often columns are found sickleform in cross section. (Later examination reveals the fact that whereas the circular sections contain but a single vascular bundle and its secondary thickenings, the sickleform ones invariably have two or more distinct primary bundles with the rays between.) These practically always divide ultimately into members assuming this same circular appearance.

Since there is no set order followed that can be discovered from external characteristics, the phenomenon of this splitting must be investigated internally. The only available matter published on this subject is a series of articles by Jost appearing in the Botanische Zeitung, 1890, and all references to the various forms he investigated will be referred to by page without repeating the entire reference each time after the first. My most satisfactory work was done with free-hand sections, treated with KOH and mounted in glycerine. Though some successful imbedding in paraffin was accomplished through the carbon disulphid process, the stained slides were more difficult to elucidate than the others, and proved of less value for actual study.

If we take a specimen like FIG. 1*a*, which shows, natural size, a piece of the rhizome and the leaf bases of the aerial shoot, and examine successive cross sections, we shall be able to trace this separation from the individual main stem of the aerial shoot down to the complete circle of separate columns, as shown in FIG. 2. The places where all successive sections described in this series are cut, are indicated on FIG. 1. The first section (PLATE 13, FIG. 3) shows a regular primary stem structure. The hollow center is surrounded by four rows of parenchyma cells, outside of which is a circle of separate open collateral bundles. These primary bundles consist of xylem, cambium, phloem, with a heavy stereome cap, outside of which are five rows of cortical parenchyma cells, surrounded by a

single-layered epidermis. Jost mentions the fact that "the aerial stems of so many Ranunculaceae show only a slight growth in thickness and develop no interfascicular cambium."* Farther down we find a complete cambium ring, through the activity of which the radial length of the primary bundles has been increased, not so much in xylem and phloem elements as in parenchyma, 4–7 rows of which are found on each side of the cambium. This has pushed the stereome cap farther out in the cortex, and we also find a periderm beginning to form to replace the epidermis. The secondary thickening in this and later sections is formed by a cambium that produces one ring of elements annually. This is anomalous to some extent, since it forms much more parenchyma than sieve or xylem ducts. The reason for this fact cannot be absolutely proved, but there may be a water storage function for all these thin-walled cells, which a xerophyte might very readily utilize. The cambium (FIG. 4) next produces weak secondary xylem elements outside of the primary xylem (which is flanked on both sides by stereome), followed by about five rows of equilateral parenchyma cells and five rows of brickshaped cells. The general change in shape suggests the spring and fall cells in wood, and probably owes its existence to the same slowing down in growth at the end of the growing season.

Outside of the cambium much parenchyma and a few sieve cells have been produced. In the outer cells of this closely packed cortex, separating it from the loose, irregular peripheral cells, appears a single row of cells with slightly thickened lateral walls, which makes a complete circle of the stem and forms an endodermis. Some of the primary cortex with its masses of stereome has become broken up, probably due in part to growth pressure from within. There is a darkening of the pith around the hollow center, which indicates necrosis of the tissues. In the next lower section (FIG. 5), which shows three years growth in thickness, we find the parenchyma which surrounds the first year xylem assuming the irregular appearance of the cortical parenchyma. A circle of cells exactly similar to the endodermis has formed inside, cutting off from the rest of the wood the xylem of the original bundles, enclosing the

*Jost. Die Zerklüftungen einiger Rhizome und Wurzeln. Bot. Zeit. **48**: 484. Jl 1890. (On *Aconitum Lycoctonum*.)

necrotic pith. Undulations appear in the outer endodermis, one of which develops into a deep cleftlike projection through the rays between the bundles and toward the center of the stem, from which the inner endodermis extends out to meet it. By the union of these the stem is divided on one side. This phemomenon may occur simultaneously in more than one radius, thus dividing the section into several parts. But in each case this method holds good, and in each case either one radial bundle mass is separated off into a circular column, or more are cut off into a sickleform group.

In his discussion of splitting in *Gentiana cruciata*,* Jost describes the division as being due to the separation of parts, by a row of newly originating cork-covered parenchyma cells, which he calls "periderm." This he considers to be a single layer of cells that have been separated off and become corky, not in any way to be considered phellogenetic in origin. The pith also is cut off by an inner periderm originating from a cork cambium, which pushes out into the wood parenchyma between the fusion bundles in order to meet this "cortical periderm." This "periderm" as described, exactly agrees with the "endodermis" found in *D. scaposum*.

Following the invasion of the central necrotic region by the endodermis, the parenchyma isolated between the two sides of the cleft dies and forms a continuous link between the necrotic areas from center to periphery. In response to the death of the tissue there is the formation of a cork layer similar to wound periderm, which protects the living tissues inside from the decaying surrounding tissues. Jost also corroborates this interpretation when he says, in speaking of *Gentiana cruciata* and *Corydalis nobilis*,† that the periderm is the consequence of necrosis of tissues, and the necrosis of tissues in both cases must have an inner cause. We find cork formation taking place on all sides of the split-off columns.

This cast-off periderm on the outside easily disappears in the earth. But in cases where we find a complete circle of columns still seemingly bound in one trunk (FIG. 2), the rotting central "bark" cannot be cast off and necessarily accumulates. This large mass of dead material can hardly be all attributed to cork forma-

* Jost. Loc. cit. p. 43.

† Jost. Loc. cit. p. 476.

tion, from the excessive amount and comparative protection of the parts thus clothed. Part of its bulk must of necessity arise from the necrotic parenchymatous pith and primary bundles cut off in the center. And careful examination of the dead elements found here, shows ducts, spiral and reticulate, as well as many fibrous pieces made up of stereome strands.

Jost believes that each old year's wood, as it becomes useless for water conduction or ceases to be in direct connection with the present year's annual growth, is cut off from the living functioning parts by this circular periderm formation, and dies, thus adding to the bulk of necrotic tissue and lessening the area of activity. Jost describes minutely this phenomenon in several cases. In *Gentiana cruciata*,* as secondary growth continues, forming new wood and cortex, old tissues are constantly cut off by an ever originating parenchymatous periderm and the significance of this periderm is to separate the functionless wood and bast in the rhizome and root from the living. In *Corydalis Ochroleuca*,† only those bundles are kept that are in direct union with leaf parts. The rest die off, and jagged parenchyma strands in the wood, by turning brown and dying, form the splits. In *Aconitum Lycoctonum*‡ (as in *Gentiana*) under symmetrical cork formation about the living tissues, and with parenchyma cells cut off that become corky about dying tissues, never more than two years' growth is left active. Periderms formed later are either concentric with the first or contribute to further splitting as already described. In *Sedum*,§ old years are all cut off by the periderm, and only the one youngest ring remains active. In *Delphinium*, such wholesale destruction apparently does not exist. No necrosis, cutting off bundle elements, can be found before the second year, and in no older form is less than two years' growth active.

In a rhizome showing four years of xylem (FIG. 6) the primary xylem is disintegrated, in the center directly outside of the necrotic pith region, and is cut off from all the rest of the wood by heavy cork zones that have particularly strong inner rims, and surround each a different one of the five columns of the split rhizome. Each

* Jost. Loc. cit. pp. 444, 461.
† Jost. Loc. cit. p. 477.
‡ Jost. Loc. cit. p. 490.
§ Jost. Loc. cit. p. 504.

one of these columns (PLATE 14) directly inside of the cork layer, has a circular region of irregular, loose parenchyma (not disintegrated to the extent of becoming brown, however). In this loose tissue the secondary xylem elements can be seen separated out from the third and fourth year elements, all three of which are surrounded by a complete ring of endodermis. This endodermis marks the outer limit of the regular close cortex, and may become, as secondary wood and parenchyma are produced inside, so stretched out and pushed into outer cortex, that it becomes the seat of activity for the production of a new cork region as the disintegrating cortical cells invade this central portion farther.

This column (as shown in PLATE 14) is not perfectly rounded. But the presence of a very active meristematic zone inside of the former inner endodermis cutting off cells on the inner side, seems to account for the final rounding off of these separate members.

Owing to the necrosis of tissues in the center of older parts, it is impossible to determine with any degree of accuracy where rhizome ends and root begins. To follow out the root changes we must begin, as in the case of the stem, with the youngest parts. The lower end of one of the final divisions, in cross section, shows a diarch root arrangement (FIG. 8), with the axial strand small but developed apparently in centripetal order, since the larger ducts are in the center, the smaller toward the outside; also since longitudinal sections show the same order of duct formation—spiral toward the outside, pitted toward the center.

Secondary thickening follows by the activity of a complete cambial ring, which cuts off collateral xylem elements and phloem opposite the primary bundle strands, and radial rows of parenchyma cells in all the remaining space. In the third layer from the outside of the regular parenchyma cells, appears the single endodermal row of cells, as in the shoot, cutting off the spongy parenchyma from the inner regions. When three years' xylem shows in a section cut farther back (FIG. 9), the central strand is surrounded by an endodermis and parenchymalike active cells. The loose cortical parenchyma invades the center through the groove made by the entering of the outer endodermis, and the root is divided. The periderm surrounds the root, and in turn each division is completely protected by an active cork layer.

There is, then, complete correspondence in the method of splitting in rhizome and root.

In general it can be said that originally in the young seedling, rhizome and root must have been continuous and undivided. As secondary thickening, accompanied by abnormal changes in central and peripheral tissues, took place, necrosis occurred in the center and to a slight extent on the outside. Longitudinal sections show that the central disintegration is very irregular, being a wide region narrowing down at each end to a small neck which opens into another larger cavity, etc. Jost claims that there is a correspondence between the leaf position and the bundle courses, and between the bundle courses and the splitting. So far as this material can be examined, there seem to be no remaining leaf traces to affect the bundle course, which is apparently straight down through the rhizome and continued in the root. But as has been mentioned before, the columns always contain finally a single bundle strand. This column must necessarily continue its own existence independently, and it is apparently quite capable of doing so, having, as it does, an active outer cambium zone, which in successive years may circle farther and farther around inside of the limiting endodermal layer, perhaps finally forming, with the meristematic parenchyma on the inside, a complete ring around the column. No material of the age I have, shows such a complete ring, but in the four year old stage we have a very close approach to this state.

To summarize briefly the order of splitting for the rhizome, which is followed exactly in the root, we can say:

1. There is regular primary shoot structure.

2. The cambium ring produces annually some xylem and phloem tissue, but much parenchyma in the normal place of these elements. An endodermis ring appears between the outermost spongy cortex and the regularly formed outer parenchyma. Periderm surrounds the whole.

3. In the third year, an inner endodermislike ring cuts off the primary xylem and parenchyma enclosing a necrotic pith, from the rest of the tissues.

4. The outer endodermis pushes down between the xylem masses, joins the inner ring of like structure, making one con-

tinuous ring about each of the segments into which the rhizome is thus divided. The tissues cut off in this way become necrotic. Columns formed are each surrounded by an active cork-forming periderm, they continue an independent existence and never exceed the number of the original bundles.

This anatomical study of the rhizome and root of *Delphinium scaposum* was carried on in the Botanical laboratories of Barnard College, Columbia University, under the direction of Dr. Herbert M. Richards, to whose inspiration and helpful suggestions the success of this investigation is mostly due. The writer wishes also to express her thanks to Dr. D. T. MacDougal for furnishing the material, and to Dr. Tracy E. Hazen and Dr. P. A. Rydberg for their assistance in determining the identity of the plant studied.

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Explanation of plates 13 and 14

FIG. 3. Cross section of primary aerial stem, showing regular primary structure, bundle ring, hollow center, stereome.

FIG. 4. Cross section of rhizome in second year, showing irregular outer parenchyma with groups of stereome, outer endodermal ring separating regular and irregular cortex, cambium ring between 2nd xylem and phloem, slight necrosis around hollow center. Space outside 1st xylem shows ring of "fall" parenchyma cells. Periderm formed.

FIG. 5. Cross section of rhizome in third year, showing inner endodermis cutting off xylem of first year with enclosed irregular parenchyma and necrotic pith. Outer endodermis projected between xylem strands meets inner endodermis, dividing the rhizome into two parts. Other grooves appear in outer endodermis, indicating subsequent divisions.

FIG. 6. Cross section of rhizome in fourth year, showing separate columns cut off each with separate periderm, endodermis, cambium, etc. Center of section shows necrotic parenchyma tissue and disintegrating xylem ducts of first year. Second year xylem enclosed in irregular parenchyma that eventually disintegrates. Large air cavities in among broken cells of cortex.

FIG. 7. Detail of column as indicated in FIG. 6, showing irregular parenchyma and second year xylem, endodermis and parenchyma cells of inner endodermis, and brickshaped cells of third year xylem.

FIG. 8. Cross section of ultimate division (root). Diarch order with second year collateral bundles produced, connected by cambium ring. Axial strand in center. Root endodermis like shoot.

FIG. 9. Cross section of third year root. Xylem of first year cut out by inner and outer endodermis, becomes necrotic. Groove marks first break in root. Periderm formed as in shoot.

FIG. 10. Detail of endodermis of third year rhizome.

FIG. 3–10 inclusive (except 7) magnified about 8 diameters. FIG. 7 magnified 38 diameters.

All plan drawings made with Edinger apparatus, Leitz oc. I, obj. 1a; FIG. 7, oc. I, obj. 2.

KEY

air	air cavities	*P*	phloem
c	cambium	*par*	parenchyma
c.p.	cortical parenchyma	*per*	periderm
end	endodermis	*s*	stereome
epi	epidermis	*x*	xylem; x_1—xylem of first year, etc.
i. end	inner endodermis		
n	necrotic tissue	*x.d.*	xylem duct

Notes on certain species of Muhlenbergia

F. Lamson-Scribner

MUHLENBERGIA COMATA (Thurb.) Benth. Jour. Linn. Soc. **19**: 83. 1881

Vaseya comata Thurb. Proc. Acad. Nat. Sci. Phila. **1863**: 79. 1863.

The genus *Vaseya*, established upon this species, is characterized by Dr. Thurber as follows: "Panicula coarctata. Spiculae uniflorae, herbaceo-membranaceae. Glumae uninerves florem adaequantes. Callus obliquus, comam pilorum paleis aequilongam gerens. Palea inferior trinervis in aristam gracilem attenuata; superior aequilonga, acuminata. Stamina 3. Ovarium stipitatum. Styli ultra medium pilis stigmaticis longis simplicissimis instructi. Squamulae . . . Caryopsis . . . ." (Thurber l. c.)

The description of the species follows: "*V. comata*, a native of the plains of Nebraska, is a perennial grass, with the aspect of *Muhlenbergia* or of a *Polypogon*, but with a coma of silky hairs around the flower as in *Calamagrostis*. Culm a foot and a half high from a creeping rhizoma, retrorsely pubescent at the node. Sheaths scabrous, equaling the internodes; ligule short, fringed, leaves 3 to 4 inches long, dull green, rough on both sides. Panicle lead-colored, about 3 inches long; the branches solitary, appressed, densely many-flowered. Spikelets very short-pediceled, compressed, pubescent, a line and a half long. Glumes narrow, very acute, serrulate on the keel, the lower a little the longer. Awn rough and flexuose, purplish, three to four lines long." (Thurber l. c.)

A rather stout erect perennial 3–5 dm. high from creeping scaly rootstocks, with simple culms, flat leaves, densely flowered oblong or cylindrical panicles and awned spikelets 3–4 mm. long; culms very finely pubescent at the nodes and for a short distance below them with reflexed hairs; sheaths glabrous, the lower ones more or less compressed; leaf blades mostly erect, rather firm in texture, 6–15 cm. long, the lowermost shorter, acute or attenuate-pointed; panicles ovate-oblong or cylindrical, 2–10 (usually about 7) cm. long, densely flowered and more or less lobate, lead-colored,

pale green, light straw-colored or rose tinted; glumes 3–4 mm. long, subequal, narrowly lanceolate or linear, acuminate, sometimes pointed with a short awn, aculeolate-scabrous on the keel excepting near the base, as long as or slightly exceeding the lemmas; lemmas lanceolate, thin-membranaceous, copiously hairy near the base; hairs 1.5–2 mm. long; awns very slender, scabrous, 2–7 mm. long, paleas lanceolate-acuminate, acute or minutely 2-toothed, nearly as long as the lemmas and similarly hairy near the base.

This species is represented in the National Herbarium by specimens from Colorado, Wyoming, Montana, Idaho, Utah, Nevada, Arizona, Washington, Oregon, and California. Specimens from the Rocky Mountain region generally have lead-colored panicles as in the type, those from Washington, Oregon, and California have pale green or very light straw-colored ones, while some of the Californian specimens have violet or rose tinted panicles. These last may prove to be separable as a distinct species.

Among the numbered specimens of this species in the National Herbarium are the following:

COLORADO: *C. F. Baker 945*, 1901; *Shear and Bessey 1339, 1514*, and *1533*, 1898; *H. N. Patterson 157*, 1885; *J. Wolf 1092*, 1873.

WYOMING: *Merrill & Wilcox 294, 365, 370, 388*, and *423*, 1901; *Aven Nelson 3857*, 1897; *T. A. Williams 2889*, 1897.

UTAH: *C. A. Purpus 6375*, 1898; *M. E. Jones 5731a*, 1894.

ARIZONA: *M. E. Jones 6056*, 1894.

NEVADA: *S. Watson 1289*, 1868.

MONTANA: *P. A. Rydberg 3411*, 1896.

WASHINGTON: *A. D. E. Elmer 558*, 1897.

OREGON: *Leiberg 617*, 1894; *W. C. Cusick 2447*, 1900; *Griffiths & Morris 514*, 1901.

CALIFORNIA: *Bolander 1097; J. G. Lemmon 5475*, 1890; *Bolander 6094* and *6101*, 1866.

MUHLENBERGIA PAUCIFLORA Buckley, Proc. Acad. Nat. Sci. Phila. **1862**: 91. 1863

M. sylvatica Pringlei Scrib. Bull. Torrey Club **9**: 89. 1882.

M. neo-mexicana Vasey, Bot. Gaz. **11**: 337. 1886.

M. Pringlei Scribn. Trans. N. Y. Acad. Sci. 14. 1894, and Vasey in Contr. U. S. Nat. Herb. **3**: 71. 1892.

Original description: "Culmo subdecumbente 12–18 pollicari; foliis convolutis apice setaceis glabriusculis; vaginis internodio parum brevioribus; ligulis membranaceis linearibus subobtusis; paniculis 2–3 pollicaribus interruptis paucifloris; glumis ovatis acutis aequalibus subcarinatis valvula 2/3 brevioribus; valvulis lanceolatis inferiore valde 3-nervia et longe aristata; spiculis rufescentibus; carinis et nervis subviridescentibus.

"Hillsides Western Texas.

"Panicle terminal with short appressed branchlets of 4–6 flowers each of a brownish red color, bristles longer than the flowers." (Buckley l. c.)

Dr. Gray (Proc. Acad. Nat. Sci. Phila. **1862**: 334. 1863) says that Buckley's *M. pauciflora* is "described from a scanty depauperate specimen of Wright's *no. 732*." This number is represented in the National Herbarium and according to the ticket was "collected in Expedition from Western Texas to El Paso, New Mexico, Oct., 1849." The specimen is branched at the lower nodes, which show a malformation apparently caused by a mite, and it is probable that the branching of the culms in this specimen is due to these insect attacks. The effect of insect work is further manifest in a more or less imperfect development of the panicle and spikelets. Similar specimens were collected in the Guadaloupe Mts. of western Texas by Dr. V. Havard in 1881. In both Wright's and Havard's specimens the glumes are broadly ovate, barely acute or abruptly short-cuspidate at the tip, and about half the length of the lemmas, which are naked at the base. The entire absence of hairs at the base of the lemmas is a further indication of abnormality in this case. In apparently healthy and normal plants the slender wiry erect culms are unbranched, the panicles rather more densely and abundantly flowered, the glumes are somewhat longer and with long-subulate points often equaling the lemmas, which are barbate on each side at the base with a dense tuft of very short hairs. The type of *M. neo-mexicana* Vasey from Las Vegas, New Mexico, and of *M. sylvatica Pringlei* from the Santa Rita Mts. of Arizona, collected by C. G. Pringle in 1881, are normally developed specimens of the species *M. pauciflora*, although Pringle's specimens are immature. The original description of *M. sylvatica Pringlei* differs somewhat from

that of *M. pauciflora*, doubtless due to the condition of the specimens as noted above. "Culms densely caespitose, terete, erect, simple, rather rigid, about 1 ft. high. Leaves involute, filiform, about 7 to each culm, minutely scabrous outside, especially towards the tip, strigose scabrous within, 4–6 in. long, the lower ones shorter; ligules broader than the leaves, decurrent along the sheath, ½ line long, irregularly cut, continued on each side into two lanceolate, acute teeth or auricles one line long. Panicle slender, contracted, 2–3 in. long, rather densely flowered. Empty glumes nearly equal, 1-nerved, with slender acuminate points, 1 line long. Flowering glume nearly or quite smooth at the base, 3-nerved, scabrous on the keel above, 1½–2 lines long, terminating in a slender awn 4–6 lines long. Palea nearly equaling its glume.

"Dry cliffs, Santa Rita Mountains, alt. 7,000 ft. July. [*Pringle*] *480*." *

There are two sheets of specimens in the National Herbarium, collected and labeled by Dr. Vasey himself, *M. neo-mexicana*, one from Watrous, New Mexico, 1884, and one from Las Vegas, New Mexico, collected in 1886. On both tickets there is written in Dr. Vasey's hand "published in Bot. Gazette, Dec., 1886."

In the original description of *M. neo-mexicana* the type is not indicated. Probably several specimens were consulted in drawing up the diagnosis, for the range is given as "New Mexico and Arizona," and the culms are described as "mostly branched near the base from thickened nodes." The Las Vegas specimens have simple culms while the Watrous specimen is branched as described by Vasey, and this specimen is assumed to be the type of his species.

Among the numbered specimens in the National Herbarium referred to *M. pauciflora* Buckl. as here understood are the following:

TEXAS: *C. Wright 732*, 1849.

COLORADO: *Frank Tweedy 391*, 1896.

NEW MEXICO: *E. O. Wooton 1047*, 1893; *F. S. Earle 164*, 1900 (culms branched, panicles strict, 5–10 cm. long); *E. W. D. Holway*

* The "*no. 480*" here cited was a private number for the collection made by Pringle in 1881 and is not the *no. 480* of his distributed sets of 1884.

21, 1896; *M. E. Jones 37a bis*, 1884; *H. H. Rusby 465*, 1880; *E. O. Wooton 333*, 1897; *E. N. Plank 36*, 1895.

ARIZONA: *F. X. Holzner 2177*, 1893; *D. T. MacDougal 779*, 1891; *G. C. Nealley 168*, 1891 (much like the type of *M. pauciflora*); *Griffiths & Thornber 170*, 1902; *Griffiths 7351*, 1904; *Griffiths 7227* and *7229*, 1904; *Griffiths 6029*, 1903; *J. G. Lemmon 410*, *J. G. Emersley 15* and *17*, 1890 (panicles 12 cm. long; glumes with long attenuate bristlelike points); *G. C. Nealley 167*, 1891 (the bristlelike tips of the glumes nearly equaling the lemmas in some of the spikelets in others only about one half as long).

MEXICO: *C. V. Hartman 754* and *793*, 1891.

MUHLENBERGIA PARISHII Vasey, Bull. Torrey Club **13**: 53. 1886

M. sylvatica californica Vasey, Bot. Gaz. **7**: 93. 1882.
M. glomerata brevifolia Vasey, Bot. Gaz. **7**: 92. 1882.
M. californica Vasey, Bull. Torrey Club **13**: 53. 1886.

Muhlenbergia sylvatica californica and *M. glomerata brevifolia* were published simultaneously by Dr. Vasey in 1882. In 1886 the same author raised both these supposed varieties to specific rank, the first, *M. sylvatica californica*, he named *M. Parishii*, and the second, *M. glomerata brevifolia*, he called *M. californica*.

The description which appears under *M. glomerata brevifolia* Vasey (Bot. Gaz. **7**: 92. 1882) is as follows: "Culms 1–2 ft. high, erect and leafy, leaves (5–8 on each culm) rigid, short and wide (2–4 in. long 2–3 lin. wide) somewhat scabrous; panicle spikelike, interrupted and with longer branches below; glumes and palets about equal in length (1 line); glumes acuminate, scabrous-puberulent; flowering glumes acuminate and tipped with an awn half its length or less, 3-nerved, pubescent below; palet acute about equaling the flowering glume."

No types are mentioned by the author for either *M. Parishii* or *M. californica*, but they were both collected in San Bernardino County, California, by the Parish Brothers, in 1881, the first distributed under *no. 1076* and the second under *no. 1028*. The specimens so numbered in the National Herbarium must be regarded as the types, *no. 1076* being the type of the species as here

treated, although *no. 1028* represents the usual form as shown by more recently collected material, for example *nos. 2113* and *2116*, collected by S. B. Parish in 1890, both from the region of the San Bernardino Mountains.

The following is a description of the species *M. Parishii* as here understood:

An erect, rigid, rather stout glabrous perennial 4–6 dm. high, from creeping woody rootstocks, with many-jointed culms, fasciculate-branched at the base, flat, scabrous leaves, densely flowered contracted panicles, and scabrous spikelets 3–4 mm. long. Culms minutely scabropubescent for a short distance below the nodes; nodes usually seven; sheaths mostly longer than the internodes, terete or slightly compressed, scabrous; ligule about 1 mm. long, lacerate and subciliate on the margins; leaf blades usually erect or ascending, rather rigid, very acute, 3–12 (usually 5–7) cm. long, 3–8 (usually about 5) mm. wide, the margins more or less revolute in drying; panicles 6–12 cm. long, lanceolate or linear in outline, more or less interrupted below; branches of the panicle erect or appressed, solitary or the lower in pairs, densely flowered to the base, or the longer lower branches naked below; spikelets broadly lanceolate, somewhat compressed, crowded and more or less glomerate, sessile or on very short pubescent pedicels; glumes broadly lanceolate, acute, acuminate, or pointed with a short awn, rather firm in texture, scabrous, strongly so on the prominent midnerve excepting near the base, nearly equal, as long as or a little shorter than the lemmas; lemmas broadly lanceolate, 3–4 mm. long, scabrous, copiously hairy near the base with hairs about 1 mm. long, awned or nearly awnless; awn when manifest rarely exceeding 2 mm. in length; palea broadly lanceolate or oblong, acute or minutely 2-toothed at the apex, hairy near the base and similar in texture to the lemma. The hairs at the base of the lemmas and paleas vary in length and in abundance but are always conspicuous.

Allied to *M. Lemmoni* Scribn. but differing in the stouter culms, broader leaves, and larger and more scabrous spikelets.

No. 1076, Parish Brothers, from the San Bernardino Mountains of Southern California, collected in July, 1881, and now in the National Herbarium, is assumed to be the type. A second, and the only other specimen in the National Herbarium, was collected in 1882 by the Parish Brothers and distributed under the same number (*1076*). They both represent luxuriant forms of Vasey's *M. californica*, differing only in a more rank development of the

culm and leaves, due doubtless to peculiarities of environment. The culms are 6–8 dm. long, leaves 10–18 cm. long, and panicles 10–16 cm. long. In all essential characters they are identical with *M. californica* and we have no hesitation in uniting the species.

MUHLENBERGIA LEMMONI Scribn. Contr. U. S. Nat. Herb. 1: 56. 1890

M. huachucana Vasey, Contr. U. S. Nat. Herb. 3: 69. 1892.

Original description: "Culms much branched below, slender, erect or decumbent, 30–45 cm. high; leaves 2.5–7.5 cm. long, 2 mm. wide, acuminate; panicle spikelike, 5–12.5 cm. long, interrupted below, the upper branches sessile, the lower pediceled and subdivided, sometimes 2.5–5 cm. long, erect; spikelets about 3 mm. long without the awns; empty glumes ovate-lanceolate, awn-pointed, nearly equal and but little shorter than the flowering glume, which is hairy below and with an awn half as long as itself. Ballinger (Runnels Co., Tex.) (G. C. Nealley)." (Scribner l.c.)

Type, *G. C. Nealley 726*, 1890, in National Herbarium. The sheet containing this specimen has also a ticket upon which "Type No. 1079" is inscribed.

The original description of *M. huachucana* is very similar to the above. It is as follows: "Culms tufted, much branched at the base, 12–18 in. high, leafy; leaves 4–6 in. long, 2 lin. wide, erect, rather rigid, scabrous; panicle 2–4 in. long, narrow, the lower branches sometimes in twos, all densely flowered, erect, contiguous; spikelets 2 lin. long, sessile; empty glumes about equal, 1½–2 lin. long, ovate, acuminate-pointed, the long points scabrous; flowering glumes about 3 lin. long, 3-nerved, with a short awn; palet about as long as its glumes. Both flowering glume and palet villous-pubescent below. Huachuca Mountains, Arizona, J. G. Lemmon." (Vasey.)

The type of *M. huachucana* is not indicated by the author of that species, but there are two specimens in the National Herbarium so named by Dr. Vasey himself both of which were collected by J. G. Lemmon, one in July 1882, *no. 2915*, Huachuca Mts., Arizona, the other in 1883, *no. 392*, Arizona, without other data.

The first specimen collected, *no. 2915*, is assumed to be the type. It agrees throughout with the type of *M. Lemmoni*, and is certainly identical with that species.

Revised diagnosis of *M. Lemmoni:*

A slender, wiry, erect or ascending, leafy perennial, 3–5 dm. high from creeping woody rootstocks, with narrow flat scabrous leaves, strict, densely flowered panicles and short-awned or awnless spikelets, 3–4 mm. long. Culms fasciculately branched at the base, very minutely scabropubescent at and for a short distance below the nodes; sheaths terete, usually exceeding the internodes in length, glabrous or minutely pubescent towards the base; ligule about 1 mm. long, more or less lacerate, ciliate on the edge; leaves 7–8 on each culm, 2–5 cm. long, 1–3 mm. wide, minutely strigose-pubescent above, scabrous on the back, revolute in drying, with slender attenuate tips; panicles 5–10 cm. long, main axis triangular or compressed, scabrous, the lower branches often in pairs, 1–2 cm. long, the upper usually solitary and flower-bearing to the base, all erect or appressed; spikelets densely crowded and more or less glomerate on very short pubescent pedicels; glumes broadly ovate-lanceolate, abruptly acuminate and subaristate or pointed with a short awn, varying to lanceolate and gradually acuminate, nearly equal, as long as or a little shorter than the lemmas, scabropubescent on the keel above, glabrous towards the base; lemmas 3–3.5 mm. long, broadly lanceolate or ovate, minutely 2-toothed at the apex, rather densely villous from near the middle to the base; awns 1–2 mm. long, occasionally reduced to a mere mucro, very rarely 5–6 mm. long; palea broadly lanceolate or oblong, about equaling the lemmas, villous in the lower half.

This species is represented in the National Herbarium by the following specimens:

TEXAS: *G. C. Nealley 132*, 1892; *no. 397* from the Chico Mts., 1889 (a nearly awnless form); *G. C. Nealley 726*, the type.

ARIZONA: *J. G. Lemmon 392*, 1883 (plant a little coarser than usual and panicles more densely flowered); *Lemmon 2915*, 1882, from the Huachuca Mts. (type of *M. huachucana* Vasey); *Canby 58*, 1894 (resembles the following specimens collected by Wilcox, in having awns 5–7 mm. long). Specimens from the same region collected by Dr. T. E. Wilcox, distributed without number, have awns 5–10 mm. long. This is a form apparently connecting *M. Lemmoni* with the next species.

MEXICO: *Pringle 395*, 1885; *Pringle 8263*, 1889, from the

Federal District, alt. 8500 ft.; *Pringle*, 1893 (lemmas barely mucronate-pointed and scabrous near the tip, a form approaching the allied *M. Parishii*).

Muhlenbergia polycaulis Scribn. sp. nov.

A slender, wiry, erect, or ascending, glabrous, leafy perennial, 3–4 or 5 dm. high, from creeping rootstocks, with linear attenuate-pointed, scabrous leaves, slender, rather densely flowered panicles, and long-awned spikelets 3–4 mm. long; culms terete, fasciculately branched at the base, glabrous or minutely scabropubescent below the nodes; sheaths scabrous, terete, longer than the internodes; ligule about 1 mm. long, ciliate on the edge and more or less lacerate; leaves about 7 on each culm, 2–6 cm. long, 1–2 mm. wide or less; panicles 5–10 cm. long, main axis scabrous, flattened or triangular and somewhat flexuose; branches solitary or the lower ones in pairs, the lowermost somewhat remote and 2–4 cm. long, the upper shorter and approximate, all erect or appressed; spikelets not crowded as in *M. Lemmoni*, the longer branches naked below, pedicels scabropubescent, nearly equaling or much shorter than the spikelets; glumes subequal, a little shorter than the florets, broadly ovate-lanceolate or lanceolate, very abruptly mucronate or short-awned, scabropubescent on the keel above, smooth below; lemmas broadly lanceolate, minutely 2-toothed at the apex, densely villous in the lower half; palea lanceolate-oblong, nearly equaling the lemma in length and similarly villous in the lower half; awn very slender and hairlike, more or less flexuose, 10–24 (usually about 20) mm. long.

Type, *C. G. Pringle 1414*, 1887.

Closely allied to *M. Lemmoni*, but more slender, with narrower leaves, long-awned and less crowded spikelets.

This species is represented in the National Herbarium by the following specimens:

TEXAS: *S. B. Buckley*, no number.

ARIZONA: *C. G. Pringle 480*, 1884 (not *480* of the collection of 1881); *Griffiths 7036*, 1904. Panicle more loosely flowered than in the type, and glumes purplish.

MEXICO: *Pringle 394*, 1885; *Pringle 1414*, collected on dry shaded ledges, Sierra Madre Mts., State of Chihuahua, Sept. 30, 1887; *Pringle 394*, 1885; *E. Palmer 592* and *724*, 1896.

Muhlenbergia curtifolia Scribn. sp. nov.

A slender wiry perennial, 1–2 dm. high, fasciculately branched at the base from creeping rootstocks, with short rigid leaves, linear panicles and short-awned spikelets 3–3.5 mm. long; culms pubescent below the nodes; leaves 7–10 on each culm, rather crowded near the base, the upper more distant; sheaths, excepting the upper ones, longer than the internodes, pubescent, especially toward the base; ligule less than 1 mm. long, ciliate on the edge; blades 1–2.5 cm. long, 2 mm. wide or less, pungent at the acute apex, scabropubescent on both sides; panicles 4–8 cm. long with erect appressed branches 1–3 cm. long or less, the main axis triangular or compressed, scabropubescent; spikelets on short, slender, pubescent pedicels; glumes lanceolate acute, subequal, a little shorter than the florets, scabrous at the tip and along the keel near the apex; lemmas broadly lanceolate, villous from just above the middle to the base, scabrous near the apex, gradually tapering into a slender scabrous awn 1–3 mm. long; palea as long as the glume and similarly hairy.

Type, *Marcus E. Jones 6047j*, 1894, collected between Kanab and Carmel, Utah, alt. 6,000 ft.

Muhlenbergia curtifolia Griffithsii Scribn. subsp. nov.

More slender throughout and wholly glabrous, with the narrower leaves spreading or deflexed and the linear panicles loosely few-flowered.

Type, *David Griffiths 5837*, 1903, collected in Du Chelly Canyon, Arizona.

U. S. DEPARTMENT OF AGRICULTURE,
WASHINGTON, D. C.

A Pliocene flora from the Coast Ranges of California

HAROLD HANNIBAL

(WITH PLATE 15)

GENERAL REMARKS

The origin and development of the California floras, particularly the peculiar xerophytic chaparral, has been a problem of no small interest to students of phytogeography. The occurrence in the Coast Ranges of a recognizable Pliocene flora, the only thing of its kind known in North America consisting entirely of living species, partly mesophytic and partly xerophytic in character, throws an interesting light upon the antiquity of these floras and suggests a possible explanation of the isolation of boreal and arctic plants on the upper slopes of high mountains of the state far south of their normal ranges.

THE SANTA CLARA FORMATION

WORK OF PREVIOUS WRITERS

The Santa Clara formation was named and described by Cooper[1] in 1894. The deposit was considered to be of lacustrine origin and referred to the Pliocene on the basis of its general lack of consolidation, the gentle tilting of the beds, and the large percentage of recent species in the molluscan fauna. It had been previously described in some detail by Lawson,[2] however, who also regarded it as Pliocene in age, but of delta origin. The portion lying in the Santa Cruz Quadrangle has been discussed by Arnold[3] and again by Branner, Newsom, and Arnold,[4] its distribution being shown in map form. Recently Jones,[5] solely on lithological grounds, has tentatively suggested its contemporaneity with what has been termed by Lawson and Palache[6] as the Orindan forma-

[1] Proc. Calif. Acad. Sci. **4**: 171. 1894.
[2] Bull. Dept. Geol. Univ. Calif. **1**: 151. 1893.
[3] Proc. U. S. Nat. Mus. **34**: 355. 1908.
[4] Santa Cruz Folio, U. S. Geol. Surv. 6. 1909.
[5] Bull. Dept. Geol. Univ. Calif. **6**: 71. 1911.
[6] Bull. Dept. Geol. Univ. Calif. **2**: 371. 1902.

tion, and earlier by Cooper[7] as the Contra Costa, a fresh-water deposit of late Miocene age in the Berkeley Hills. The faunal evidence does not bear out such a correlation.

CHARACTER AND DISTRIBUTION OF BEDS

The formation consists of a well-bedded series of clays, slits, and sands with minor gravel strata, of wide extent, underlying and outcropping about the edges of the Livermore, Santa Clara, and San Benito valleys. A large mass fills a formerly extensive depression southwest of Mt. Hamilton, of which San Felipe Valley is a part. Remnants extend south as far as Cook P. O. in San Benito County, a distance of nearly a hundred miles from Livermore. The occurrence of sediments about Portola, thirty miles west of the latter point, indicates a considerable breadth at this latitude. The northward extension of the former lake is uncertain, since the sinking of the San Francisco Bay region in comparatively recent times has permitted the burial of its sediments beneath the valley alluvium.

The thickness of the series is not inconsiderable, but varies widely. In the foothills near Tres Pinos fully 1,000 feet of nearly horizontal strata overlie the Miocene, while the top of the series is cut off by erosion. A section down Calabazas Cañon in the Santa Cruz Mountains, without exposing the basal beds, was estimated to be 3,000 feet in thickness to a point where the upper strata are similarly absent.

It is highly probable that the entire Santa Clara formation was deposited at or comparatively near sea level. The character of the flora furnishes proof that the elevation could hardly have been greater than 1,000 feet and was probably much less. It is difficult to conceive that a single body of water, or quite as probably several connected bodies, of this extent could exist at any considerable elevation in proximity to the ocean continuously for a sufficient period of time to deposit over half a mile of sediments without draining the lake by stream corrosion alone. The enormous thickness of the beds is perhaps explainable on the assumption that the valleys acted as catchment basins with the bottoms sagging beneath the load of sediments. It might be added that

[7] Proc. Calif. Acad. Sci. 4: 169. 1894.

there is a general tilting of the strata toward the middle of each of the three valleys.

The source of the waters which supplied this vast lake, and the outlet to the ocean are uncertain. The large proportion of coarse material in the southern portion of the San Benito Valley suggests that a stream of no small size entered here. It is by no means improbable that the vast expanse of water was kept up by the run-off of the Great Valley of California, through the precursors of the Sacramento and San Joaquin rivers. The lake doubtless fluctuated widely and a considerable proportion of the sediments about the border may have been deposited under fluvial conditions.

FAUNA

Aside from the plant remains, the formation contains a fauna consisting almost entirely of aquatic mollusca,[8] of which a large percentage, six out of ten species, still exist in the waters of northern California.

In the following list the species marked with an asterisk are living.[9]

* *Anodonta cygnea impura* Say
Gonidea angulata Cooperi Arnold
Sphaerium sp. nov
* *Corneocyclas compressa* Prime
* *Planorbis trivolvis* Say
* *Physa "heterostropha* Say"
"*Carinifex*" *Sanctae-clarae* Hannibal
* *Paludestrina longinqua* Gld.
"*Amnicola*" *Yatesiana* Cooper
* *Valvata "virens* Tryon"

[8] Mr. John Hain, of Cook, California, obtained a leg bone of an extinct Proboscidian from these beds near Tres Pinos. So far as the writer is aware no other recognizable mammal remains have been found in the formation.

[9] Names in quotation marks are subject to revision in a forthcoming paper on the fauna of the Santa Clara formation. *Amnicola Yatesiana*, which in reality belongs to the allied genus *Phyrgulopsis*, is confined to these beds. The genus appears to be valuable for horizon determination in the later Tertiary fresh-water deposits of California.

GEOLOGIC RELATIONS

The youngest formation antedating the Santa Clara is the Purisima, a marine deposit, older Pliocene in age. The Purisima is confined chiefly to the ocean front, but an embayment extended from Half Moon Bay and Pescadero across the Santa Cruz Mountains past La Honda and Portola to the hills near Stanford University and the mouth of Stevens Cañon, while another arm extended inland from Santa Cruz to the vicinity of Chittenden.

The relation of the Santa Clara to the underlying Purisima formation, along the flanks of the Santa Cruz Mountains is probably one of decided unconformity, though the incoherence of the beds has prevented its actual observation. The tilting of the Purisima, which is apparently somewhat greater than that of the Santa Clara, and the differences in distribution of the two indicate that important structural movements took place in the interval previous to the opening of the Santa Clara period.

The older Pliocene through the Coast Ranges appears to have been a period of peneplanation. The movements which preceded the Santa Clara epoch developed the general outlines of the present topographic features. The relief of the mountain ranges was, however, far more gentle than at present, and the elevations of the mountains themselves decidedly less.

Since the deposition of the Santa Clara, several important geologic events have taken place in the history of the Coast Ranges.[10] Following the Santa Clara sedimentation, apparently without the intervention of any other deposits, the entire Coast Ranges were lifted more or less bodily, carrying the old lake level to an elevation of perhaps 4,500 feet above the sea. Rapid erosion ensued and the soft lacustrine beds were cut into deeply, far below the present valley floors. This period of intense elevation and erosion called the Sierran epoch, was widespread in California. It is regarded as marking the opening of the Quaternary, corresponding at least in part to the Glacial epoch of elevated or more northern regions. Subsequently a period of depression ensued, succeeded by temporary oscillations, which have continued to the present. The beds of the Santa Clara formation in the San Benito Valley

[10] Lawson, A. C. Bull. Dept. Geol. Univ. Calif. 1: 115, 242. 1893. Smith, J. P. Science II. 30: 346. 1909.

and about Evergreen and Los Gatos in the Santa Clara Valley now reach an elevation of 1,200 to 1,500 feet.[11]

The unconformable deposition of the valley alluvium upon the Santa Clara has taken place more or less continuously since the close of the Sierran epoch. At Madrone, as an alluvial fan of the Coyote River, it reaches the maximum elevation of 345 feet.[12] At least a portion of the alluvium must be referred to the Quaternary from the presence of mammal remains characteristic of that age in gravels near Mountain View.[13] Hence it must not be assumed that the Sierran epoch, though a very long period, was coincident with the entire Quaternary.

The latest event, and a purely local one, has been the sinking of the San Francisco Bay region, causing a flooding of the Golden Gate River system by the tides. As a result the Santa Clara sediments reach an elevation of not more than 500 feet at Mission San Jose, north of that point they largely disappear beneath the later alluvium.

AGE OF THE FORMATION

The Santa Clara formation may be regarded as having been deposited during late Pliocene time. It occupies an unconformable position upon the Purisima, a marine formation of older Pliocene age. It contains a molluscan fauna of which two-thirds of the species are still living. The strata were intensely elevated and eroded subsequent to their deposition, during the Sierran epoch, early Quaternary.

The Santa Clara is presumed to be contemporaneous with the Deadman Islands formation of San Pedro Harbor, Santa Monica Cañon, and Packard's Hill, Santa Barbara, a marine deposit occupying an analogous stratigraphic position in southern California.

LOCALITIES WHERE PLANTS WERE OBTAINED

Plant remains are abundant almost everywhere in the Santa Clara formation, but recognizable material has been obtained

[11] In the vicinity of Bird Creek, near Hollister, the beds, in a disturbed condition, reach an elevation of 1800 or 1900 feet. This is probably produced by local conditions, due to the proximity of the San Andreas fault, along which the earthquake of 1906 took place.

[12] Branner, J. C. Jour. Geol. **15**: 3. 1907.

[13] Santa Cruz Folio, U. S. Geol. Surv. **1909**: 6.

from only five localities, and by far the larger part was derived from two. No doubt careful search would have revealed many more and would materially extend the flora, but the incoherent character of the beds restricts collecting to fresh exposures, to be found only in cañons and gorges. Furthermore, collecting is possible only during the summer and fall months after the matrix has dried out sufficiently to stand transportation to the laboratory.

The localities are as follows:

PORTOLA: gulch below Holliday's ranch in creek-cut about 1,000 feet above mouth of gulch, ⅓ mile south of Portola, Santa Cruz Mountains. The mollusk beds just below this point have been known for a number of years to the Stanford University Geological Survey. Plant beds were found by the writer in 1908. Subsequently collections were made in 1909 and 1910, and in connection with Dr. J. P. Smith and party of students in 1910.

STEVENS CAÑON: creek-cut just above "big camp ground," a flat planted with *Eucalyptus* trees, about 1½ miles above mouth of gorge, Stevens Cañon, Santa Cruz Mountains. Found by W. G. Hannibal, the writer's father, in 1909. Subsequently visited in connection with Dr. Smith and party of students, 1910. The material consists almost solely of *Salix* and lignitized wood.

CALABAZAS CAÑON: "reef" in creek bed at nose of bend above second wagon bridge, ¼ mile from mouth of gorge, Calabazas Cañon, Santa Cruz Mountains. Found by the witer in 1908, subsequent collections made in 1909 and 1910, in connection with Dr. Smith and party of students in 1910, and with Mr. H. M. Edson of Palo Alto in 1910.

SOLLY RANCH: near a spring tunnel on Solly Ranch north of Bird Creek, ¾ mile west of old dairy on mesa above San Benito River, and 4 miles southwest of Hollister, Gavilan Range. This locality was discovered a number of years ago by the owners of the ranch when digging for water. A specimen is contained in the collection of the late Miss Annie R. Laws, now the property of the Geological Museum at Stanford University. The locality was visited by the writer in 1908 and again in 1910 with Mr. Edson. All the best material was derived from the tunnel.

BEAR VALLEY: forks of a small gulch below limestone hill, over ridge 2 miles northeast of Cook P. O., Bear Valley, Gavilan

Range. Mr. John Hain, an old resident of Bear Valley, interested in natural history, pointed out this locality to Dr. C. H. Gilbert a number of years ago. It was subsequently visited by Dr. Smith, Mr. Fordyce Grinnell, Jr., and the writer in 1907, and by the writer in 1910. The main exposure apparently represented an old tule bed, consisting of an interlacing mass of indeterminate carbonized stems in peaty clay. Farther up the same branch of the gully a few fairly well preserved leaves were obtained.

LIST OF PLANTS OBTAINED FROM THE SANTA CLARA FORMATION

	Portola	Stevens Cañon	Calabazas Cañon	Solly Ranch	Bear Valley
Alnus rhombifolia Nutt.	A		X	A	
Amelanchier alnifolia Nutt.			X		
Arbutus Menziesii Pursh	R				
Arctostaphylos Manzanita Parry	R		R		
Cephalanthus occidentalis L.	R		X		
Cercocarpus betulaefolius Nutt.			R		
Cornus glabrata Benth.			A		R
Grossularia Menziesii (Pursh) Cov. & Britt. (?)	R		X		
Padus demissa (Nutt.) Roem.	R		X		R
Pasania densiflora (Hook. & Arn.) Oerst.	A		X		R
Populus trichocarpa Torr. & Gray	A				
Pseudotsuga taxifolia (Poir.) Britt. (?)			R		
Psoralea physodes Dougl.			X		
Quercus agrifolia Née			R		
Quercus chrysolepis Lieb.	X		A		
Rhamnus californica Esch.			R		
Rhamnus Purshiana DC.	X				
Salix fluviatilis Nutt. (?)			A		
Salix laevigata Bebb	A	A	A	R	
Sequoia sempervirens (Lamb.) Endl.	X				

A abundant, X not common, R rare.

NOTES ON SPECIES[14]

PINACEAE

Pseudotsuga taxifolia (Poir.) Britton. Douglas spruce.

A single badly water-worn cone unlike that of any other western conifer is referred with doubt to this species.

A common conifer in the yellow pine belt, particularly the upper portion, and fog belt. British Columbia and South Dakota south to Monterey County, California, northern Mexico, and western Texas.

[14] Determinations have been made in each instance by comparison with recent material in the Stanford University Herbarium.

Sequoia sempervirens (Lamb.) Endlicher. (PLATE 15, FIG. 3.) Redwood.

The characteristic species of the fog or redwood belt of the Coast Ranges. California-Oregon boundary to Monterey County, California.

SALICACEAE

Salix laevigata Bebb. Bebb willow.

Occurs along streams, its zonal distribution being determined by stored water rather than by rainfall. Siskiyou County, California, to northern Lower California.

Salix fluviatilis Nuttall. Long-leaf willow.

The resemblance of the leaf parts of *S. exigua*, *S. argophylla*, and *S. fluviatilis* renders it impossible to decide which of the three the series at hand should be referred to. It is not generally agreed that the several members of the *fluviatilis* group represent more than a single polymorphic species.

Sand bars along valley streams. British Columbia, Mackenzie Basin, and southeastern Canada south to Lower California, northern Mexico, and the District of Columbia.

Populus trichocarpa Torrey and Gray. Black cottonwood.

Several of the specimens show the characteristic anastomosing venation and cordate bases of leaves from young shoots.

Along foothill streams in moist situations, usually with *Acer californicum* and *Fraxinus oregona* in central and northern California. Occurs from southern Alaska east to Montana and south to San Diego County, California.

BETULACEAE

Alnus rhombifolia Nuttall. (PLATE 15, FIG. 6.) White alder.

Occurs along foothill and low mountain streams. Eastern Washington and Idaho south to San Diego County, California.

FAGACEAE

Pasania densiflora (Hook. & Arn.) Oerst. (PLATE 15, FIG. 8.) Tanbark oak.

The venation of this species is unmistakable.

Characteristic of the yellow pine and fog belt, but extending

a short distance beyond Sequoia into the chaparral belt. Southwestern Oregon to Santa Barbara and Mariposa counties, California.

Quercus chrysolepis Liebmann. (PLATE 15, FIG. 2, 9.) Cañon oak.

Several acorn cups and a large series of leaves, nearly all of the small smooth form from mature trees, are at hand.

A characteristic member of the more humid portions of the chaparral belt. Southwestern Oregon to northern Lower California.

Quercus agrifolia Née. Live oak.

A species of wide zonal distribution, occurring in the redwood, yellow pine, foothill, and chaparral belts. Mendocino County, California, to northern Lower California.

GROSSULARIACEAE

Grossularia Menziesii (Pursh) Coville & Britton. Cañon gooseberry.

A number of specimens agree fairly well with this species. The identification is a doubtful one, however, since the leaves of the members of this genus are not readily distinguishable.

Stream banks, southern Oregon, south nearly to San Francisco Bay in the Coast Ranges.

ROSACEAE

Cercocarpus betulaefolius Nuttall. Birch-leaf mahogany.

A typical chaparral shrub. California-Oregon boundary south to northern Lower California.

MALACEAE

Amelanchier alnifolia Nuttall. Western serviceberry.

A single specimen having the strong frequent venation and smooth margin of the form called *A. pallida.*

Chaparral belt. Alaska east to Lake Superior, south to California-Mexico boundary and New Mexico.

AMYGDALACEAE

Padus demissa (Nuttall) Roemer. Western chokecherry.

The impressions show little of the serrated margins character-

istic of this species. This is due doubtless to state of preservation, since it is more or less true of the other serrate species as well.

Best developed in the more humid portions of the chaparral belt, but extends into more arid portions on the one hand and into the redwood and yellow pine belts on the other. Northern British Columbia east to the Rockies and south to northern Lower California.

FABACEAE

Psoralea physodes Douglas. Chaparral psoralea.

Several imperfect specimens of the broad-leaved form were secured.

Characteristic of the more humid portions of the chaparral belt. Humboldt to Los Angeles counties, California.

RHAMNACEAE

Rhamnus Purshiana De Candolle. (PLATE 15, FIG. 10.) Cascara sagrada.

The material at hand shows no tendency to intergrade with the following species though the latter is regarded by some as a subspecies of *R. Purshiana*.

Cañons and river bottoms of the fog belt. Puget Sound region and Idaho south to Mendocino County, California.

Rhamnus californica Eschscholtz. (PLATE 15, FIG. 7.) California coffeeberry.

Occurs chiefly in the intermediate zone between the fog belt and chaparral belt, frequently on open hillsides, but extending into the chaparral with *Arbutus*. Humboldt County, California, to northern Lower California.

CORNACEAE

Cornus glabrata Bentham. (PLATE 15, FIG. 4.) Bentham's dogwood.

Most of the Calabazas Cañon material shows a pair of strong lateral veins near the base of the leaf. The character is more pronounced than in most of the herbarium material examined. The specimen figured retains traces of the original leaf structure.

Foothill streams in rather moist situations. Humboldt County south to Monterey County, California.

ERICACEAE

Arbutus Menziesii Pursh. (PLATE 15, FIG. 1.) Madrono.

The character of the venation in the only specimen obtained is decidedly more infrequent than usual in this species. It is possible that additional material will necessitate its specific separation.

Best developed with the redwood, but extends into the chaparral, yellow pine, and foothill belts. Southern British Columbia to southern California.

Arctostaphylos Manzanita Parry. (PLATE 15, FIG. 5.) Common manzanita.

Two specimens from different localities belong to *A. Manzanita* or one of the nominal species grouping with it. Discrimination cannot be made on the leaf parts alone.

A typical chaparral plant. Overlaps with *Sequoia* along the edge of the fog belt. Ranges from near the Oregon-California line east into the northern Sierra Nevadas and south to Mt. Tamalpais, California.

RUBIACEAE

Cephalanthus occidentalis Linnaeus. Button bush.

Several leaves, all of which show more numerous secondary veins than usual in this species.

Occurs along borders of lowland streams and ponds. Oregon and southeastern Canada to Mexico and Florida.

CONCLUSIONS

COMPARISON WITH OTHER FLORAS

The obvious feature in a comparison of this with other fossil floras is its very recent character. So far as the material might be identified every species is living in the Coast Ranges today. It is distinctly unlike the older Tertiary floras of the west, since their contents, palms, laurels, broad-leaved oaks, etc., are types indicating moist, nearly tropical conditions. The floras of the middle and upper Miocene are as yet largely undescribed.[15] From

[15] Lesquereux, L., Proc. U. S. Nat. Mus. **11**: 35. 1889, has reported *Diospyros virginiana* L. var. *Turneri* Lesq., *Magnolia californica* Lesq., *Laurus* cf. *canariensis* Heer, *Viburnum* cf. *rugosus* Pers., and *Vitis* sp., and F. H. Knowlton in Turner, H. W., Jour. Geol. **6**: 498. 1898, notes *Populus* sp., *Alnus* sp., *Castanea* sp., *Vaccinium* sp., and *Arbutus* sp. from Kirker's Pass near Mt. Diablo in the San Pablo

these some recent species may be expected and a comparison can then be made. However, the important changes in climate and humidity, which took place in the continental history of California at the opening of the Pliocene[16] have gone a long way toward eliminating these types. With their extinction appeared full-fledged and apparently unheralded, the modern California flora. It is obvious that the several peculiar genera and numerous species which characterize it could not have come into existence and become fixed types in the brief interval, geologically speaking, between the upper Miocene and late Pliocene. It is reasonable to assume that this flora, already developed to its present high specialization, immigrated from elsewhere, where, through a very considerable period of time, it had evolved.

The Santa Clara flora cannot be compared with other floras of corresponding age, since no other Pliocene floras have been described from North America.[17] Such floras occur in England[18] and other parts of Europe, but consist entirely of local species. Quaternary plants are known in the Loess of Canada[19] and the marine deposits of Maryland[20] but are likewise too remote to afford comparison.

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formation, Upper Miocene, associated with *Astropadsis Whitneyi* and other characteristic marine mollusca. No magnolias or chestnuts are now indigenous to California, and but few of the other species have any living relations west of the Rocky Mountains.

[16] While the stratigraphic relations of the Contra Costa and Kettleman Lake beds are known with considerable certainty, of the entire faunas, totaling some twenty species of fresh-water mollusks, only two, *Anodonta cygnea impura* and *Paludestrina longinqua*, are common to the two formations. These occur again in the Santa Clara beds and still exist, widespread, from southern Oregon east to the Rocky Mountains and south well into Mexico. The other Contra Costa species suggest strongly the fauna living in the lower Mississippi Valley. The Kettleman fauna on the other hand is the precursor of the existing central California fauna.

It seems probable that the abrupt change of conditions which eliminated the Miocene flora was coincident with that which eliminated the Miocene fresh-water mollusca. The latter took place during the comparatively brief interval separating the Contra Costa and Kettleman periods of sedimentation, and it is presumed the former did also.

[17] Knowlton, F. H., Jour. Geol. **18**: 116. 1910, has reported *Woodwardia* sp., *Sassafras* sp., and *Sterculia* sp. from the Falls of the Columbia River, in beds said to be of Pliocene age.

[18] Reid, C., & E. M. Jour. Linn. Soc. **38**: 206. 1908.

[19] Dawson and Penhallow. Bull. Geol. Soc. Am. **1**: 311. 1890.

[20] Hollick, A. Pliocene and Pleistocene. Md. Geol. Sur. **1906**: 148, 217.

All the species live today in the Coast Ranges of California north of San Francisco Bay. Indeed one familiar with the plants of that region would immediately identify this flora with that which inhabits the valleys of Sonoma, Mendocino, and Humboldt counties a few miles from the ocean in the zone of overlap of the redwood belt (Transitional zone) and chaparral belt (Upper Sonoran zone). That it does not show the extreme humid conditions of the open coast is evident from the presence of such species as *Alnus rhombifolia*, and species of *Cercocarpus* and *Arctostaphylos*. On the other hand *Sequoia* delineates it as at least partially fog belt in aspect.

EVIDENCE OF A COLD EPOCH

This flora agrees very well with the evidence of the aquatic mollusca and points to perceptibly colder conditions in central California during Pliocene time, but makes it certain that this cold facies was due not to elevation, but to actual migration of isotherms. Such a condition could not have been a local phenomenon but was probably widespread on the Pacific Coast.

This offers an explanation of the isolated occurrence of numerous arctic and boreal plants on the tops of high mountains far south of their normal distribution. The Santa Clara period was succeeded by the Sierran epoch, when the entire coast seems to have been carried by a great orogenic uplift many hundreds of feet above its present elevation. Very little is known of the climatic conditions which existed in California at that time. The rapid erosion prevented the formation of extensive lakes, and later depressions have carried all the marine deposits of the period even deeper beneath the ocean. This page, torn from the otherwise complete geologic record of the late Cenozoic of the coast, probably corresponds at least partially to the Glacial epoch elsewhere. Hence it is commonly assumed to have been colder and more humid than the present. It seems probable that the northern plants continued to exist south of their present southern limits during the early Quaternary, as a result of the cold epoch, the high elevation, the effects of which would be similar, or both, and were finally isolated toward the close of the Sierran epoch in the middle Quaternary.

ACKNOWLEDGMENTS

Acknowledgments are due first of all to Dr. J. P. Smith, at whose suggestion this study was undertaken, and whose interest and ever ready criticisms have made results possible. Dr. W. R. Dudley and Dr. LeRoy Abrams have permitted the free use of the Stanford University Herbarium, assisted in making identifications, and contributed everything in their power toward the writer's interest. Mr. James McMurphy, from his familiarity with the flora of the northern Coast Ranges, has also been of material assistance in the matter of determination of material. The plate is reproduced from photographs taken by Mr. John Howard Paine.

STANFORD UNIVERSITY,
CALIFORNIA.

Explanation of plate 15

(All figures are approximately natural size.)

FIG. 1. *Arbutus Menziesii* Pursh, Portola.
2. *Quercus chrysolepis* Lieb., Calabazas Cañon.
3. *Sequoia sempervirens* (Lamb.) Endl., Portola.
4. *Cornus glabrata* Benth., Calabazas Cañon.
5. *Arctostaphylos Manzanita* Parry, Calabazas Cañon.
6. *Alnus rhombifolia* Nutt., Solly Ranch.
7. *Rhamnus californica* Esch., Calabazas Cañon.
8. *Pasania densiflora* (Hook. & Arn.) Oerst., Portola.
9. *Quercus chrysolepis* Lieb. (inside cast of acorn cup), Portola.
10. *Rhamnus Purshiana* DC., Portola.

A supplemental description of Euphorbia ephedromorpha

H. H. Bartlett

The original description of *Euphorbia ephedromorpha* was drawn up from flowering specimens collected by Mr. C. C. Deam, in January, 1905, near Gualan, Guatemala. Mr. Deam has since supplemented the type material by specimens collected in June, 1909, at the original locality. The specimens collected in January have no leaves (FIG. 1); those collected in June are in full leaf (FIG. 2) but show no trace of the caducous cymes. With the ample material of this anomalous plant, which is now available, it is possible to supplement the incomplete original diagnosis and to correct certain serious misconceptions regarding its relationship and morphology. *Euphorbia ephedromorpha* is not, as formerly stated to be, a member of the section Alectoroctonum. It cannot be placed in any of the sections defined by Boissier in de Candolle's Prodromus, and so far as a careful search of the literature has shown, no species related to it have been described. A new section, Ephedromorpha, is proposed for its reception, to be ranged with the five of Boissier's sections of *Euphorbiae appendiculatae* which are characterized by the presence of stipular glands.

Euphorbia§ Ephedromorpha sect. nov.

Shrubs with winged stems. Leaves ample, deciduous, alternate, with two minute stipular glands at the base of the pet ole on either side of the flower bud. Cymes compound (i. e., main axis arrested by a cyme, not by a single involucre); bracts filiform-spatulate, opposite, only one of each pair bearing an axillary branch. Involucral glands plane, ovate, with entire appendages. Seeds foveolate.

Species two, Central American and Mexican. (The second species, represented in the Gray Herbarium by fragments too poor to serve as a type, was collected at Cerro Quiengola, Oaxaca, Mexico, *Caec. & Ed. Seler 1611.*)

Euphorbia ephedromorpha Bartlett, Proc. Am. Acad. **43**: 56. 1907.

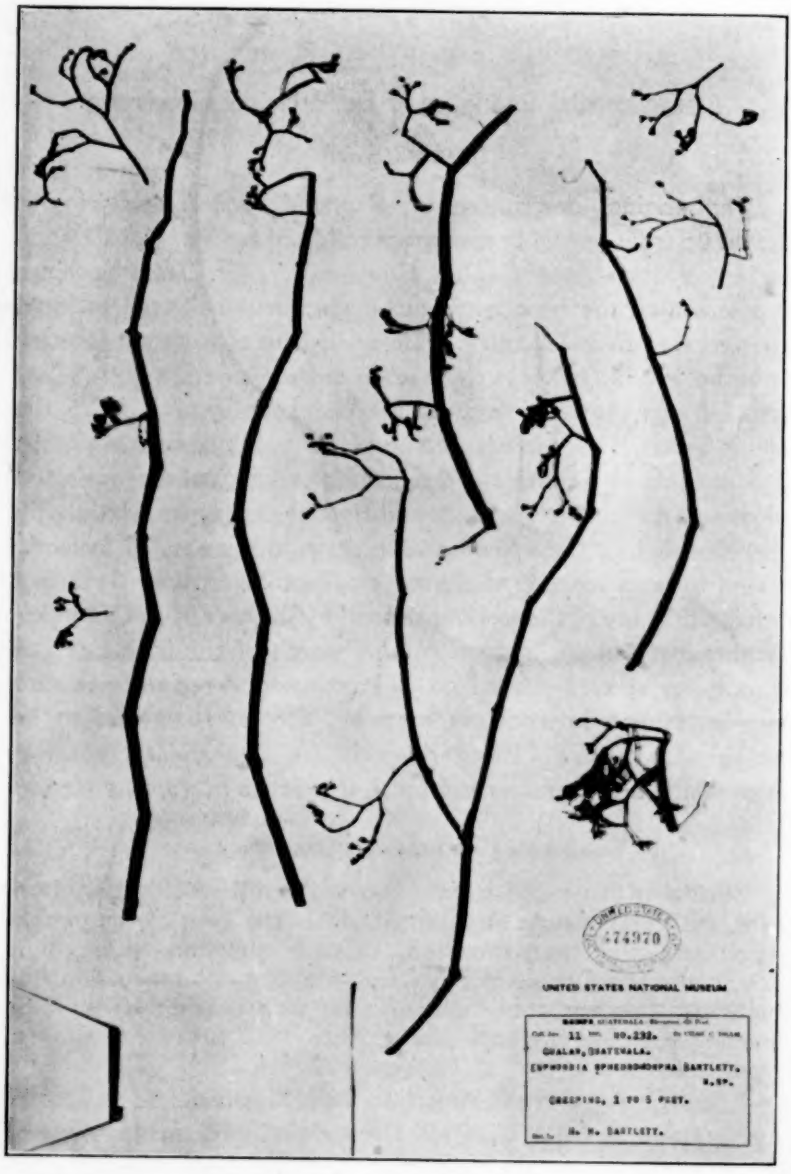

FIG. 1. *Euphorbia ephedromorpha*, in flower, × 1/3.

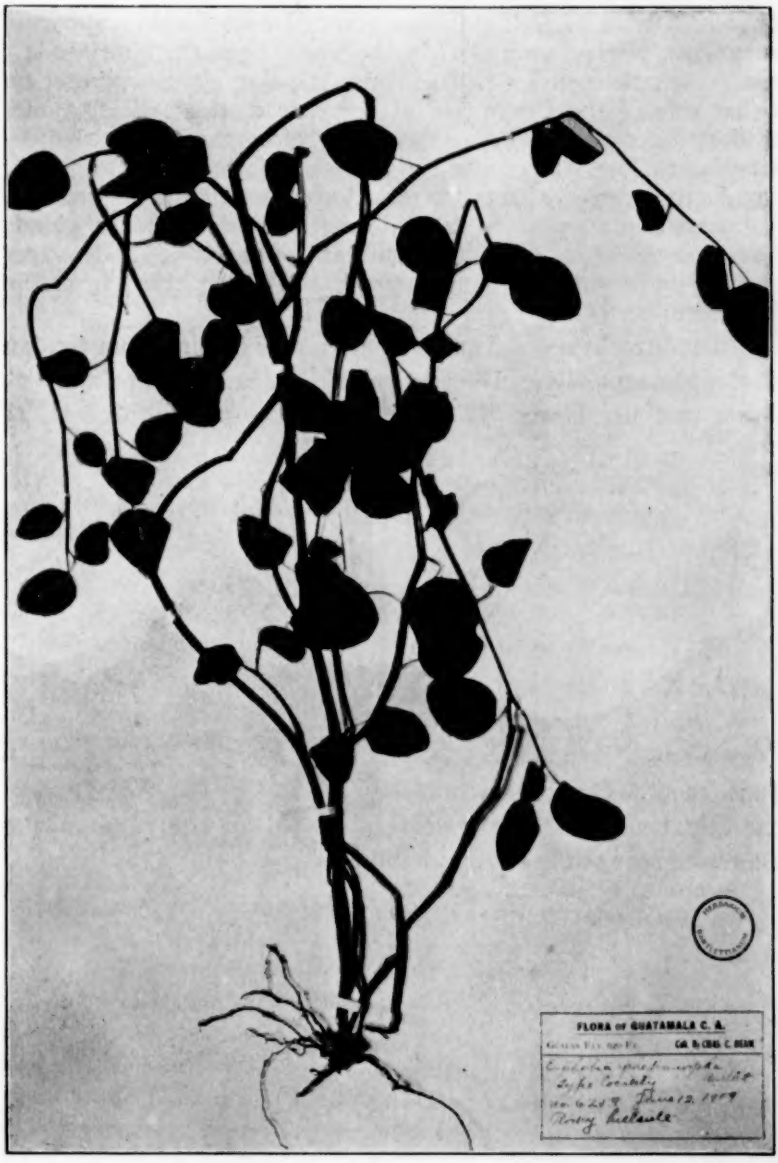

FIG. 2. *Euphorbia ephedromorpha*, in full leaf, × 1/3.

Shrub; branches prostrate or ascending, a meter long, sparsely branched, wing-angled, glabrous, green; leaves deciduous, ovate, somewhat pilose, especially on the veins beneath, blades 2–4.5 cm. in length, petioles half as long; stipular glands minute, on either side of the flower bud at the base of the petiole; cymes axillary on the old wood, expanding before the leaves, densely glandular-pilose, as are also the minute filiform-spatulate bracts; involucres narrowly conic, 3 mm. long, equaling their pedicels, segments five, very short, flabelliform, digitately laciniate, glands five, bearing oblong or slightly spatulate, entire, white appendages (FIG. 3); ovary 2 mm. long in fruit, slightly exserted from the involucre; seeds lilac gray, ovoid, foveolate.

In nude rocky dry soil at the side of a road leading from Gualan to the Motagua River, Department of Zacapa, Guatemala, *C. C. Deam 232* (in flower, 11 Jan. 1905) and *6529* (in full leaf, 14

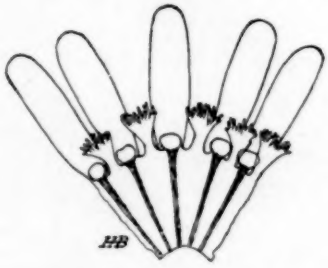

FIG. 3. Involucre of *Euphorbia ephedromorpha*, × 10.

June 1909). On leafless branches of *Euphorbia ephedromorpha* the stipular glands are quite obliterated at the edge of the depressed scar of the caducous cyme.

BUREAU OF PLANT INDUSTRY,
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1907–1911

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